1 **Title:** Long-term population dynamics – theory and reality in a peatland ecosystem

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**Running headline:** Long-term population dynamics

**Summary (maximum 350 words):**

1. Population dynamics is a field rich in theory and poor in long-term observational data. Finding sources of long-term data is critical as ecosystems around the globe continue to change in ways that current theories and models have failed to predict. Here we show how long-term ecological data can improve our understanding about palaeo-population change in response to external environmental factors, antecedent conditions and community diversity.

2. We examined a radiometrically-dated sediment core from the Didachara Mire in the mountains of south-western Georgia (Caucasus) and analysed multiple biological proxies (pollen, fern spores, non-pollen palynomorphs, charcoal, diatoms, chrysophyte cysts, midges, mites and testate amoebae). Numerical techniques, including multivariate ordination, rarefaction, independent splitting and trait analysis, were used to assess the major drivers of changes in community diversity and population stability. Integrated multi-proxy analyses

are very rare in the Caucasus, making this a unique record of long-term ecological change in a global biodiversity hotspot.

3. *Synthesis.* Population changes in the terrestrial community coincided primarily with external environmental changes, while populations within the peatland community were affected by both internal and external drivers at different times. In general, our observations accord with theoretical predictions that population increases lead to greater stability and declines lead to instability. Random variation and interspecific competition explain population dynamics that diverged from predictions. Population change and diversity trends were positively correlated in all taxonomic groups, suggesting that population-level instability is greater in more diverse communities, even though diverse communities are themselves more stable. There is a continuing need to confront population theory with long-term data to test the predictive success of theoretical frameworks, thereby improving their ability to predict future change.

**Key words:** chironomids, diatoms, diversity, Georgia, palaeoecology and land-use history, pollen, population dynamics, testate amoebae

## Introduction

Improving knowledge of ecological processes is increasingly important as anthropogenic impacts affect global ecosystems in potentially irreversible ways (Parmesan 2006; Cahill et al. 2013; Kubisch et al. 2014). In a changing environment, extinction risk is an ever-present concern (Crone 2016). Population theory predicts that

84 extinction risk is reduced in populations that are stable or increasing (Channell &
85 Lomolino 2000). Growing populations are considered more resilient to environmental
86 change and demographic disruptions than shrinking ones (Lande 1993; Hamilton et al.
87 2009). In reality, however, populations and communities change in ways that current
88 theory cannot always predict (Moritz & Agudo 2013; Zhang et al. 2015).

89 The potential for observational data to shed light on long-term population dynamics is
90 widely appreciated (Moritz & Agudo 2013; Pedrotti et al. 2014; Jackson & Blois 2015)
91 but less often achieved (Birks et al. 2012; Horreo et al. 2016). Examples of population
92 dynamics that do not conform to population theory are of interest as they may
93 potentially reveal circumstances in which environmental factors, species interactions or
94 antecedent conditions override the demographic effects of population growth and
95 stability (Tilman 1996; Kuparinen et al. 2014; Ogle et al. 2015; Reyer et al. 2015).

96 Critical comparison of long-term ecological changes with independent climatic records
97 (e.g. ice cores, speleothems) could help resolve questions about extrinsic and intrinsic
98 factors affecting ecosystems (Ammann et al. 2000; Jeffers et al. 2011, 2015; Lavoie et
99 al. 2013; Seddon et al. 2015). In theory, synchronous changes are likely to reflect
100 extrinsic drivers, while asynchronous changes may reflect intrinsic processes (Lavoie et
101 al. 2013). The extent to which this actually occurs is influenced by a population's
102 growth rate, environmental sensitivity, phenotypic plasticity, genetic variability and
103 other factors (Oliver et al. 2015; Ogle et al. 2015).

104 Population dynamics and species diversity are closely intertwined. At the community
105 level, high-diversity ecosystems tend to be more stable and resilient to environmental
106 changes than less diverse systems (Tilman & Downing 1994; Cardinale et al. 2012; cf.
107 May 1972). At the population level, on the other hand, empirical data and modelling

suggest that individual populations in diverse communities should experience greater instability than those in less diverse communities (Tilman 1996; Loreau & de Mazancourt 2013). Little scientific attention has been devoted to examining this relationship temporally using palaeo-data. Knowledge of the factors that drive diversity on centennial to millennial scales is limited geographically, temporally and taxonomically (Feurdean et al. 2013; Birks et al. 2016a,b).

In this paper, we use high-quality palaeoecological data from a peatland to address the following questions:

1. Do palaeo-population dynamics correspond temporally to environmental changes (extrinsic vs intrinsic) and, if so, does this relationship differ for different groups of organisms?

2. To what extent do palaeo-population changes conform to the predictions of population theory, especially in relation to diversity?

## Materials and Methods

### *Research Design*

We adopted a palaeoecological approach to address our research questions. Biological fossils from various taxonomic groups were analysed at comparable sampling intervals in a single core to provide a long temporal sequence of palaeoecological changes in a peatland ecosystem. Palaeo-population dynamics were reconstructed based on fossil accumulation rates (Flenley 2003; Jeffers et al. 2015). We used statistical techniques that detect major changes in population size and stability for each taxonomic entity without the need for analogue-based bias corrections (Walker & Wilson 1978; Walker & Pittelkow 1981; Birks et al. 2012). Population changes were compared to

independent climatic records (regional-scale conditions) and changes in sediment composition within the site (local-scale conditions). Based on ecological theory, we predicted that populations achieve greater stability following an increase in population size (Lande 1993; Hamilton et al. 2009), and that taxonomic groups of higher diversity (richness) exhibit greater community-level stability and population-level instability compared to low-diversity groups (Tilman 1996; Loreau & de Mazancourt 2013; Gross et al. 2014).

*Study Site*

Our study site is a poor fen, Didachara Mire, located near the upper forest limit in the Lesser Caucasus (or Caucasus Minor) Mountains of Georgia (41º41'02"N, 42º29'49"E; see Fig. S1 in Supporting Information). It sits at the foot of Mt Tsvinta (2423 m) on the NW flank of the Arsiani Range at an elevation of 2000 m a.s.l. The peatland forms part of the headwaters of the Acharistskali River, a tributary of the Chorokhi (Çoruh) River. Geologically, the Arsiani Range is composed of Upper Miocene–Lower Pliocene volcanic and sedimentary units of the Goderdzi Suite (Gudjabidze 2003; Lebedev et al. 2012), which contain important fossil deposits (Shatilova et al. 2011). Differential erosion of the Goderdzi Suite, along with landslides, slumping and remnants of Pleistocene glaciation, has created a complex terrain (Maruashvili 1971). Didachara is thought to have originated as a glacial lake (Margalitadze 1982).

Didachara is an optimal site for studying environmental change as it is situated at the intersection between two global biodiversity hotspots (Caucasus and Irano-Turanian: Mittermeier et al. 2005), two distinct vegetation belts (Colchic mixed-coniferous forests and subalpine vegetation: Nakhutsrishvili 2013), and two major climatic zones (maritime and continental: Javakhishvili 1964; see Fig. S1). The peatland occupies a

small, closed basin (Fig. S2). Its predominant vegetation is a relatively species-rich *Sphagnum–Carex* association (*S. subsecundum, S. centrale, S. teres, C. muricata, C. canescens, C. inflata, C. irrigua*), with patches of *Drosera anglica, D. intermedia, Comarum palustre*, *Menyanthes trifoliata* and *Alisma plantago-aquatica*. The slopes around and below the peatland have coniferous forests dominated by *Picea orientalis* and *Abies nordmanniana*, as well as krummholz formations of *Fagus orientalis*, *Sorbus boissieri* and *Salix caprea* (Margalitadze 1982; nomenclature after Gagnidze 2005). Subalpine meadows of the West Lesser Caucasian type (Nakhutsrishvili 2013) extend from the site's elevation to the highest elevations of the nearby mountains (2452 m).

Margalitadze (1982) previously reconstructed the Holocene vegetation history of the site on the basis of undated pollen assemblages in two sediment cores. The present study greatly improves on that earlier reconstruction and is among the first of its kind in the Caucasus region to integrate dated palaeoecological data from various proxies (de Klerk et al. 2009; Moiseenko et al. 2012).

*Field and Laboratory Methods*

In August 2003, three parallel sediment cores were collected from the centre of the peatland using a Streif-Livingstone corer (Fig. S2; Merkt & Streif 1970). Core C, the most complete sequence, was selected for detailed multi-proxy palaeoecological analyses, loss-on-ignition and radiocarbon dating. In the laboratory, samples were taken at regular intervals to extract fossilised pollen, spores and non-pollen palynomorphs (0–910 cm), midges and mites (2–798 cm), diatoms and chrysophytes (610–810 cm) and testate amoebae (70–630 cm); these depth ranges were selected based on preliminary analyses and sediment characteristics. Statistically valid numbers of diatoms were only recovered in lake sediments. Testate amoebae were mostly found in peat.

179 Pollen and spores provide information on past vegetation change at regional and local
180 scales, which is itself a reflection of climatic, edaphic and ecological factors. Pollen was
181 prepared in 92 samples using standard methods, including 10% KOH, concentrated HF
182 and acetolysis treatments (Moore et al. 1991). *Lycopodium* marker spores were added to
183 calculate pollen concentrations (grains $cm^{-3}$) and hence pollen accumulation rates
184 (grains $cm^{-2}$ $yr^{-1}$). Pollen and spore identification was performed at 400× magnification
185 following published guides (Punt 1976 ff.; Reille 1999). At least 320 terrestrial pollen
186 grains were identified per sample (mean: 555). Aquatic pollen, spores and non-pollen
187 palynomorphs indicative of peatland conditions were also quantified. We used
188 microscopic charcoal particles (10–500 µm diameter) to reconstruct regional fire history
189 (MacDonald et al. 1991; Tinner et al. 1998; Colombaroli et al. 2008). Particles were
190 counted on pollen slides at 250× magnification (Finsinger and Tinner 2005).

191 Chironomids are sensitive indicators of changing freshwater environments, including
192 temperature variations (Walker 2001). Chironomids and other invertebrate remains
193 (biting midges and oribatid mites) were quantified in 48 samples. Sediment samples
194 were processed following standard techniques (Walker 2001; Brooks et al. 2007). Wet
195 sediments (1–3 g) were initially washed through a 100-µm mesh sieve. Invertebrate
196 remains were sorted and picked out from the sieve residue in a Bogorov counting tray
197 under a stereomicroscope at 25–40× magnification and mounted on microscope slides
198 using Euparal®. Chironomids were identified at 200–400× magnification following
199 Brooks et al. (2007) and Andersen et al. (2013a). Ceratopogonidae (biting midges) were
200 separated into morphotypes following Walker (2001). Only chironomids were used for
201 analyses requiring percentage data (e.g. zonation, ordination). Accumulation rates for
202 all invertebrate taxa were calculated by wet sediment weight (remains g $WW^{-1}$ $yr^{-1}$). At
203 least 55 remains were identified per sample (mean: 700).

In freshwater environments, diatoms and chrysophytes may be used to trace changes in nutrient status, salinity and pH (Smol et al. 2001). Diatoms and chrysophyte cysts were enumerated in 23 lake sediment samples. Samples were digested in $H_2O_2$ and HCl, and mounted in Naphrax following Renberg (1990). Above a depth of 735 cm at least 250 diatom frustules were identified per sample, but below this depth 110–215 valves were counted per sample due to low concentrations (mean valve count for the core: 435). Diatom accumulation rates were not estimated.

Testate amoebae are considered sensitive to changes in surface wetness and acidity in peatlands (Payne 2011; Payne 2014; Jassey et al. 2014; Lamentowicz et al. 2015). Testate amoebae were analysed in 58 samples. Preparation followed Mazei et al. (2011) and involved soaking and sieving of 1 $cm^3$ peat samples at 0.5 mm, settling for 24 hours and staining with erythrosine for microscopic examination. This method avoids physical damage to tests and loss of small specimens (Payne 2009; Avel & Pensa 2013). Identifications were made using taxonomic guides (e.g. Mazei & Tsyganov 2006) to the highest level of taxonomic precision in order to capture important morphological traits (Fournier et al. 2012; Lamentowicz et al. 2015). Accumulation rates were determined by counting all tests in the prepared samples, with a statistically acceptable minimum of 50 testate amoebae per sample (Payne and Mitchell 2009) (mean count: 815).

Sediment organic content was estimated using loss-on-ignition at temperature steps of 550 and 950 ºC (Heiri et al. 2001). Eleven samples of wood and other identifiable macrofossils were submitted for AMS radiocarbon dating. Radiocarbon dates were calibrated using the IntCal13 calibration curve (Reimer et al. 2013) and a calendar age of -53 BP (2003 AD – collection year) assigned to the core top. We produced an age–depth model (Fig. S3) using Bacon 2.2 (Blaauw & Christen 2011), a Bayesian approach that considers prior information on sedimentation rates. Stratigraphic diagrams showing

229 the relative abundance of each taxon by sample depth and modelled age were produced
230 using Tilia 2.0.32 (Grimm 2013).

231 *Numerical Analyses*

232 To analyse palaeo-community interactions and factors influencing ecosystem
233 development, we used assemblage zones and multivariate ordination scores as the basis
234 for comparison (Ammann et al. 2000). Assemblage zones were determined through
235 binary splitting, the number of zones being assessed statistically by the broken stick
236 model (Bennett 1996). Non-metric multidimensional scaling (NMDS) with Bray-Curtis
237 dissimilarity measure was applied to each of the five proxy datasets (upland pollen,
238 wetland pollen and spores, chironomids, diatoms and chrysophytes, and testate
239 amoebae). NMDS was selected over other techniques because it makes no assumptions
240 about response models and is therefore applicable to datasets of different variances.
241 Data were square-root transformed prior to analysis in PAST (Hammer 2015).

242 The study of past diversity is useful for understanding present diversity patterns and
243 making future predictions (Rull 2012). However, diversity indices are as diverse and
244 problematic as diversity itself (Mendes et al. 2008; Giesecke et al. 2014), especially in
245 palaeoecological studies (Smol 1981; Birks et al. 2016a). For this study, community-
246 level richness was estimated using constant-sum rarefaction, implemented through the
247 "vegan" package in R (Oksanen et al. 2015; R Core Team 2015). Rarefaction of
248 accumulation-rate data was also performed where applicable, following van der Knaap
249 (2009), to avoid problems of interdependence in percentage data.

250 To assess whether individual palaeo-populations have changed in consistent ways, we
251 used independent splitting, a valuable and underutilised tool for analysing multi-proxy
252 data (Lotter et al. 1995; Birks & Birks 2006; Birks et al. 2012). Independent splitting

253 treats each palaeoecological taxon independently, which is only possible when
254 accumulation-rate data and a robust age-depth model are available. Changes in
255 accumulation-rate data through time are divided (split) into sections with homogenous
256 mean and standard deviation statistics. These statistics are used to assess relative
257 changes in palaeo-population size and stability, without the need for quantitative
258 population estimates (Walker & Wilson 1978).

259 Independent splitting was implemented in Psimpoll (Bennett 2005). Pollen taxa with
260 <10 occurrences were excluded, as were testate amoeba, midge and mite taxa with <5
261 occurrences. At each statistically significant population change (Walker & Wilson
262 1978), we observed whether stability increased or decreased according to the ratio of
263 mean to standard deviation (m/sd: Walker & Pittelkow 1981). Results were compared to
264 the null model of Blaauw et al. (2010), with 450 random proxy walks of 200 samples at
265 population sizes of 500 and 2000 (representative of local proxies and terrestrial pollen
266 respectively: Blaauw et al. 2010). Observed population changes in fossil data were also
267 compared to species traits by associating fossil taxa with traits from representative or
268 similar species (Kleyer et al. 2008; Fournier et al. 2015).

269 **Results**

270 Palaeoecological data from Didachara show significant long-term variations in all the
271 taxonomic groups analysed at decadal to multicentennial scale (Fig. 1). A total of 208
272 terrestrial pollen taxa, 32 wetland taxa (local pollen and non-pollen palynomorphs), 52
273 diatom taxa and chrysophyte cysts, 61 testate amoeba taxa, 28 midge taxa and oribatid
274 mites were identified (Fig. S4). In interpreting the data, an important distinction must be
275 made between the larger spatial scale represented by upland pollen compared to the
276 other proxies which represent communities within the site itself. Pollen from major

277 pollen-producing trees in mountainous areas is readily transported upslope by wind
278 (Kvavadze 1993). Upland pollen therefore comprises a mixed signal derived from
279 source plants at varying distances from the site (typically 1–10 km: Markgraf 1980;
280 Mariani et al. 2016). Other proxies (wetland plants, diatoms, testate amoebae, midges
281 and mites) are largely derived from local, *in situ* populations. Hence upland pollen
282 provides a terrestrial community background against which to interpret local changes in
283 the lake/peatland community. In the following section, major palaeoecological
284 transitions are interpreted with reference to environmental conditions.

285 *Terrestrial community development since 13,000 cal. BP*

286 The earliest **upland palaeovegetation** zone (Poaceae-*Artemisia*; Fig. 1) indicates a
287 largely treeless landscape of grassy steppe, with moderate burning and deposition of
288 minerogenic sediments, typical of Lateglacial environments across the region (Wick et
289 al. 2003; Messager et al. 2013, 2017). Increasing temperature and precipitation at the
290 beginning of the Holocene (approx. 11,700 cal. BP; Fig. 2) allowed the lake to fill,
291 meadow and marsh vegetation to expand (Poaceae-*Potentilla* zone), and fire to increase
292 as fuel limitations decreased. Meadow vegetation was replaced by deciduous woodland
293 species (*Ulmus*-*Fraxinus* zone) around 9900 cal. BP, likely favoured by a decreased
294 impact of fire (limit zones 2-3). Today *Ulmus* and *Fraxinus* rarely occur at the upper
295 forest limit, only achieving dominance in low–middle elevation forests (Ketskhoveli
296 1971). Neither tree is a major pollen producer (Connor 2011), so it seems certain that
297 they were canopy dominants in Early Holocene vegetation around Didachara, facilitated
298 by increased temperatures and a lack of competition. *Fraxinus* was probably
299 outcompeted by the cold- and shade-tolerant *Fagus orientalis* as it expanded its range
300 around 8200 cal. BP (*Fagus*-*Ulmus* zone). Mixed coniferous-deciduous forests followed
301 around 6300 cal. BP, with *Picea orientalis* and *Abies nordmanniana* increasingly

302 important (*Picea-Abies* zone). This association is typical of the mountain forests of
303 Colchis (Western Caucasus) today (Nakhutsrishvili 2013), although the timing of its
304 Holocene establishment varies from place to place (Connor & Kvavadze 2008). Fire
305 activity in the *Picea-Abies* zone peaked at ca. 4000, 3000 and 1800 cal. BP, indicating
306 disturbances in the forest. A brief episode of deforestation followed at 950 cal. BP
307 (Poaceae-*Fagus* zone), mainly affecting coniferous forest and accompanied by an
308 increase in anthropogenic pollen indicators (Behre 1986). Human populations increased
309 in the highlands during the mediaeval period (Burney & Lang 1971), with widespread
310 ecological impacts (Connor 2011). Since 300 cal. BP coniferous forests have returned.
311 *Abies* populations have not recovered as successfully as *Picea*, being more sensitive to
312 human activities (Connor 2011).

313 Overall, significant changes in the terrestrial community's structure (assemblage zone
314 boundaries) are closely associated with regional-scale climatic changes recorded in
315 isotopic records (Fig. 2).

316 *Lake/peatland community development since 13,000 cal. BP*

317 Within Didachara's **aquatic and wetland vegetation**, sedges (Cyperaceae) were
318 dominant from 13,000 to 9900 cal. BP (Fig. 1), suggesting a shallow or fluctuating
319 water-table. Spores of dung-inhabiting fungi (i.e. *Cercophora* and *Sporormiella*)
320 suggest herbivores were present, perhaps visiting the site as a waterhole. Around 9900
321 cal. BP, as *Ulmus-Fraxinus* woodlands expanded, *Pediastrum* algae indicate rising lake
322 levels (*Pediastrum*-Cyperaceae zone). Increasing numbers of fern spores after 8000 and
323 particularly after 6300 cal. BP indicate that open water was being encroached upon by
324 wetland vegetation and the wetland surface was increasingly shaded by trees. *Sphagnum*
325 and *Menyanthes trifoliata* appear at 4000 cal. BP (fern-*Sphagnum* zone) as a peatland

326 formed in the former lake basin (Fig. 1). The return of a fern-Cyperaceae association
327 from 1400–800 cal. BP suggests a drying phase, as has been inferred for this period
328 from sites further east (Connor 2011). Higher moisture levels returned more recently
329 (Cyperaceae-*Sphagnum* zone).

330 **Diatom and chrysophyte** palaeo-assemblages are recorded from 11200–7700 cal. BP.
331 An initial succession of benthic taxa (e.g. epiphytic *Gomphonema olivaceum* and
332 epipelic *Fragilariforma nitzschioides*) suggests an initially low lake level,
333 corresponding to the final stages of steppe vegetation in the surrounding landscape. A
334 peak in chrysophyte cysts constitutes the next phase (10,960–10,800 cal. BP), perhaps
335 influenced by increased nutrient inputs as the lake filled (Smol 1985), a supposition
336 corroborated by rapid fluctuations in mineral content (Fig. 1). *Aulacoseira nygaardii*, a
337 species typical of oligotrophic lakes, peaks shortly after (10,800–10,640 cal. BP),
338 followed by a largely benthic diatom community including aerophilic species
339 (*Orthoseira roeseana)* and indicative of nutrient enriched, shallow water with limited
340 thermal stratification (*Pinnularia-Orthoseira* zone). After 9970 cal. BP, tycho-
341 planktonic *Aulacoseira nygaardii* again becomes dominant, with short-lived peaks in
342 *Pinnularia microstauron* and chrysophytes around 9300 and 8600 cal. BP. This
343 *Aulacoseira-Pinnularia* zone indicates a higher lake level and corresponds to the
344 Cyperaceae-*Pediastrum* zone in the wetland vegetation and the expansion of *Ulmus-*
345 *Fraxinus* woods around the study site.

346 Compared to other proxies, **midge and mite** palaeo-assemblages exhibit more
347 consistency over the period analysed (11,000 cal. BP onwards). *Limnophyes*, a
348 chironomid often found in semi-aquatic habitats amongst mosses and macrophytes
349 (Andersen et al. 2013b), is common in all zones except in the uppermost *Tanytarsus-*
350 *Psectrocladius* zone (Fig. 1). In the earliest zone, cool conditions are inferred until

351 10,100 cal. BP, based on the abundance of *Krenopelopia*, *Micropsectra radialis*-type
352 and other cold-stenothermic taxa (Pankratova 1977; Cranston & Epler 2013). This is
353 followed by a phase with warmth-adapted taxa (e.g. *Corynoneura scutellata*-type,
354 *Procladius*) that corresponds temporally to the *Ulmus-Fraxinus* phase in the upland
355 vegetation. Cooler conditions returned from 8100–4000 cal. BP, as *Fagus* and
356 coniferous trees extended their range in the area. The second zone (*Limnophyes-*
357 *Corynoneura*) indicates relatively warm summers from 4000 to 1400 cal. BP. Abundant
358 oribatid mite remains in this phase correspond to peat accumulation and the
359 Cyperaceae-*Sphagnum* zone in the wetland vegetation. Oribatid mites are commonly
360 associated with *Sphagnum* in the Caucasus (Murvanidze & Kvavadze 2010). The loss of
361 warmth-adapted chironomids in the third zone (1430–170 cal. BP) could indicate cooler
362 temperatures, although it is also possible that habitat changes in the wetland (i.e.
363 *Sphagnum* decline) contributed to this change. The subsequent *Tanytarsus-*
364 *Psectrocladius* zone indicates a major shift in invertebrate communities: true aquatic
365 and thermophilous chironomids increase in percentage and in absolute terms, suggesting
366 warmer and wetter conditions. At the nearby Goderdzi Pass (2025 m), meteorological
367 data show a significant temperature rise since records began in the 1960s (Westphal et
368 al. 2011; Keggenhoff et al. 2014). Diatom assemblages from the Caucasus Mountains
369 likewise record pronounced 20$^{th}$-century temperature rise (Moiseenko et al. 2012).

370 **Testate amoebae** palaeo-assemblage changes are closely linked to shifts in the wetland
371 vegetation over the period analysed (8080–500 cal. BP). The first zone (*Trinema-*
372 *Pseudodifflugia*) falls within the Cyperaceae-fern wetland phase (Fig. 1). In the Eastern
373 Mediterranean and Black Sea region, the testate amoebae identified in this zone are
374 found in fen or swamp environments with a near-surface water-table (Payne 2011). The
375 second zone (*Hyalosphenia-Pseudodifflugia*) is a wet transitional zone of only two

376 samples (6670–5740 cal. BP). The *Difflugia-Centropyxis* association that replaces it is
377 typical of minerotrophic sedge-dominated fens (Payne 2011). A major change occurs
378 around 4100 cal. BP, when testate amoebae characteristic of poor fens and *Sphagnum*-
379 dominated vegetation increase (e.g. *Nebela penardiana, Heleopera sphagni*), indicating
380 terrestrialisation. Another transitional zone (one sample) occurs between 1950 and 1850
381 cal. BP with a *Trinema lineare* peak. The last three zones track wetland vegetation
382 changes closely, with indications of greater oligotrophy during the last millennium,
383 reflecting peatland acidification linked to climate change.

384 Overall, significant changes in the lake/peatland community prior to 6000 cal. BP (lake
385 phase) are associated with changes in the terrestrial community (Fig. 2). After this time,
386 significant changes relate to shifts within the peatland community that are largely
387 independent of terrestrial community changes.

388 *Palaeo-population dynamics and diversity estimates*

389 The temporal distribution of major palaeo-population changes is shown in Fig. 2.
390 Within the terrestrial community (upland pollen), changes are concentrated around the
391 Pleistocene–Holocene transition. A second period of rapid population change occurred
392 from approx. 4500 cal. BP to the present. This coincides with terrestrialisation and the
393 increasing prevalence of *Picea orientalis* in the surrounding vegetation. Within the
394 peatland community, the various taxonomic groups (wetland vegetation, midges and
395 mites, and testate amoebae) exhibit very different patterns. Wetland vegetation follows
396 the terrestrial community pattern, albeit with a stronger reaction to terrestrialisation.
397 Midge and mite population changes are clustered during recent centuries. Testate
398 amoebae population dynamics intensify after terrestrialisation and are dominated by
399 population increases.

400 The effect of antecedent population conditions on subsequent populations is shown in
401 Fig. 3. Population theory predicts that populations should stabilise following an increase
402 and destabilise following a decrease. This pattern (Fig. 3a) is observed in 73% of cases
403 among upland taxa, 70% among wetland vegetation taxa, 71% among testate amoebae,
404 and 78% among midges and mites and these figures are relatively insensitive to the
405 exclusion of rare taxa (in which case results are 66%, 69%, 67%, and 71%). Species that
406 do not conform to these predictions ('unpredicted' in Fig 3a) have a different
407 distribution of body-size traits compared to species that exhibited the predicted response
408 (Fig. S5)..

409 Reconstructed richness trends are shown in Fig. 4. Each taxonomic group exhibits a
410 different trend in richness and no group remains stable through time. The terrestrial
411 community (upland pollen) exhibits peaks corresponding to phases in which Poaceae
412 (grasses) are prominent. Richness in the wetland vegetation group increased
413 substantially at the time of terrestrialisation. Both diatoms and chironomids show long-
414 term declines in richness, although chironomid richness has peaked in recent decades.
415 Richness among testate amoebae has increased gradually through the last 8000 years.
416 Accumulation-rate diversity estimates agree with constant-sum rarefaction results,
417 except in the case of upland pollen, which has greater accumulation-rate variability. For
418 each taxonomic group, diversity estimates through time are positively correlated with
419 the total number of population changes (Fig. 5).

420 **Discussion**

421 *1. Intrinsic and extrinsic drivers of palaeo-population dynamics*

422 In the Didachara record, significant population changes were not evenly distributed
423 through time (Fig. 2). The most prominent changes in terrestrial populations are

424 associated with rapid changes in precipitation, temperature and seasonality at the
425 Pleistocene–Holocene boundary, *ca* 11,700 cal. BP (Wright et al. 2003; Wick et al.
426 2003; Göktürk et al. 2011; Messager et al. 2013, 2017). Regional climatic shifts are
427 'slow/large' environmental changes that theory predicts would reduce ecosystem
428 resilience (Seddon et al. 2011, 2015). Our observations suggest that these changes
429 impacted upon both terrestrial and lake/peatland communities (Fig. 2). Population-level
430 reactions were particularly strong within the terrestrial community. This is perhaps due
431 to the larger spatial scale represented by the upland pollen proxy and its greater
432 sensitivity to regional-scale climate change.

433 The close correspondence between terrestrial population changes and regional climatic
434 trends supports the idea that environmental changes are primary drivers of long-term
435 community development and population dynamics (Jackson & Blois 2015; Crone
436 2016). However, climate change acting on one or more species may have initiated an
437 ecological cascade via biotic interactions with other species. Simulations and empirical
438 evidence show that biotic interactions (such as competition) may override climatic
439 controls on species abundance (Brooker 2006; Miller et al. 2008).

440 Terrestrialisation (or 'macrosuccession': van der Valk 2012) had major impacts on
441 lake/peatland population dynamics. Populations of midges, mites, testate amoebae and
442 other wetland taxa increased at the transition from shallow lake to peatland, 4500–4000
443 cal. BP (Fig. 2). Chironomid population dynamics subsequently tracked temperature
444 changes and testate amoebae population dynamics followed increasing oligotrophy (Fig.
445 S6). Community dynamics also changed during the mid-late Holocene, with
446 lake/peatland community shifts generally occurring out-of-phase with terrestrial shifts
447 (Fig. 2). This would be expected if intrinsic dynamics (such as terrestrialisation)

448 overtook extrinsic factors (such as climate) in their importance for ecosystem
449 functioning (Seddon et al. 2014, 2015; Jeffers et al. 2015).

450 Terrestrialisation was related primarily to intrinsic processes of organic matter
451 accumulation within the peatland. Its timing, however, was influenced by extrinsic
452 climatic warming, indicated by increases in thermophilous chironomid assemblages at
453 Didachara (Fig. S6), as well as isotopically and palynologically inferred temperatures
454 across the region (Wick et al. 2003; Connor 2011). Terrestrialisation was therefore
455 intrinsically driven and climatically mediated, a finding that agrees with research into
456 peatland systems elsewhere (Belyea & Baird 2006; Lavoie et al. 2013).

457 As in other parts of Eurasia (Seddon et al. 2015), we suggest that 'slow/large' processes
458 diminished in the Caucasus during the mid-Holocene (Fig. 2) and that greater resilience
459 developed in the peatland community (i.e. macrophytes, testate amoebae and
460 invertebrates). This resilience weakened around 1000 cal. BP as anthropogenic
461 deforestation impacted on the terrestrial community, creating feedbacks onto water table
462 depth (via tree removal), macrophyte cover (sunlight availability) and trophic status
463 (acidification). Responses across various trophic levels in and around the site are
464 evidence of a trophic cascade triggered by deforestation (Ireland & Booth 2012).

465 *2. Antecedent conditions*

466 A key question in ecology is whether populations, distributions or ranges change in
467 predictable ways (Brooker 2006). Population dynamics theory predicts that growing
468 populations should subsequently achieve stability, while declining populations will
469 experience greater instability (Channell & Lomolino 2000). If this were true in every
470 instance, a great number of ecological problems could be instantly solved. Allee effects

471 and other concepts are used to describe exceptions to this theory (Kuparinen et al. 2014;
472 Oliver et al. 2015).

473 Two-thirds of our observations support the key theoretical predictions of population
474 theory (Fig. 3a). The observations are remarkably uniform given that they derive from
475 mostly unrelated taxonomic groups. Random walk simulations produce similar results
476 to the fossil data (Fig. 3a), casting doubt on whether the observed differences in palaeo-
477 population response are real or artefactual. The null model has no inherent consideration
478 of species interaction or environmental forcings (Blaauw et al. 2010), factors expected
479 to influence palaeo-population dynamics at Didachara. While our results support the
480 predictions of population theory, they call for caution in attaching ecological
481 explanations to patterns that may be caused by random variation.

482 Certain fossil observations fall beyond the bounds of the random simulations (asterisked
483 in Fig. 3a). This is particularly true for testate amoebae and wetland pollen, taxonomic
484 groups at Didachara whose histories are closely intertwined. This raises the possibility
485 that community-level interaction influences population dynamics, although taphonomy,
486 life history, niche specialisation, environmental change and interspecific interaction
487 may be equally important.

488 Several limitations apply to our palaeo-population analyses. Although population splits
489 are significant, stability changes in the fossil data were not significantly different to
490 those generated by the null model. Generation and response times of testate amoebae
491 and chironomids are many times faster than terrestrial trees. Sampling intervals for
492 short-lived taxa may be inadequate to detect rapid changes in population size and
493 stability. Even generation times of terrestrial trees vary by several orders of magnitude
494 (Walker & Chen 1987).

It is unlikely that any feasible sampling interval can adequately represent all palaeo-population changes for every taxon. It may be necessary to model empirical data using Bayesian statistics (Clark & Bjørnstad 2004) to target particular taxa or groups. Such datasets could be used to identify taxa whose histories exhibit early warning signals of ecosystem change (Scheffer et al. 2009). Independent splitting results hint at population instability predicting subsequent population decline among longer-lived taxa (Fig. S7), but sampling intervals may be inadequate to address this using the current dataset.

While there is considerable replication within the Didachara record (337 palaeo-population changes), they solely relate to a single core from a single site and are dominated by terrestrial pollen changes. We encourage replication in other palaeo-records to determine the generalisability of these findings. Questions also remain regarding the degree to which population dynamics can be overridden by random variation, competition and environmental change.

We used trait analysis to gain further insight into population dynamics that diverged from theoretical predictions. Tall canopy trees are disproportionately represented among taxa that conflict with theory – they increased and subsequently experienced greater variability (Fig. S5). Competition between canopy dominants seems the most likely explanation for this pattern (Bennett 1986), as *Picea orientalis, Abies nordmanniana, Pinus kochiana* and *Fagus orientalis* all inhabit the same bioclimatic niche (Nakhutsrishvili 2013).

Low-growing taxa are most frequent among species whose populations have decreased, which reflects the replacement of low-statured Late-glacial steppes and Early Holocene meadows by taller forest vegetation. Species that do not follow the predictions of population dynamics theory, however, tend to be taller (Fig. S5). Additional height may

519 confer competitive advantages (Brooker 2006), particularly in an increasingly forested
520 environment.

521 Peatland taxa exhibit similar size-related tendencies (Fig. S5). Testate amoebae with
522 smaller apertures are more prevalent among the populations that conflict with
523 theoretical predictions (Fig. 3), including abundant taxa such as *Difflugia* and
524 *Hyalosphenia* species. Our results suggest that organism size affects population
525 dynamics (Brooker 2006; Pelletier et al. 2007) and that biotic interactions such as
526 competition may play a stronger role in ecosystem dynamics than is generally
527 acknowledged (Jeffers et al. 2015). Wider application of independent splitting to other
528 suitable palaeoecological records is likely to uncover consistent ecological responses for
529 taxa whose lifecycles are too long or cryptic to monitor using alternative methods.

530 *3. Diversity and stability*

531 Ecological theory states that greater diversity lends stability to communities (Cardinale
532 et al. 2012; Tilman et al. 2014; cf. May 1972). Upland pollen has the highest overall
533 richness in rarefaction results (Fig. 4). Over the long term, upland pollen tends to
534 exhibit relatively gradual transitions between different assemblages (Fig. S6).
535 Chironomids have the lowest overall richness and exhibit more pronounced fluctuations
536 in assemblages (Fig. S6), although fewer significant shifts in assemblage structure (Fig.
537 2). Seen through ordination results, our observations suggest that more diverse
538 communities are inclined towards greater long-term stability, but seen through numbers
539 of statistically significant assemblage shifts, the inverse is true, raising questions about
540 how best to assess long-term stability (see also Loreau & de Mazancourt 2012). Life
541 histories are also critical: it may be expected that upland vegetation composed of long-

542 lived trees may have a greater degree of ecological inertia than short-lived chironomid
543 communities (Smith 1965; Von Holle et al. 2003).

544 Richness in the various taxonomic groups has not remained stable through time (Fig. 4).
545 Peaks in richness in the terrestrial community are associated with periods in which
546 grasses (Poaceae) played a prominent role (zones 2 and 6; see Fig. 1). The lowest
547 richness is associated with forested periods (5 and 7) because of the dominance of
548 competitive, late-successional tree species (e.g. *Fagus and Picea*: Nakhutsrishvili
549 2013). The grassland zones have greater palynological evenness, a characteristic that
550 has been shown to correspond to greater habitat diversity (Feurdean et al. 2013;
551 Matthias et al. 2015). These zones were also more affected by fires (Fig. 1), which are a
552 key disturbance agent contributing to greater landscape diversity and taxonomic
553 richness in Europe (Giesecke et al. 2012; Colombaroli et al. 2013) and the Caucasus
554 (Connor 2011).

555 Within the peatland community, long-term changes in diversity are apparent in all
556 taxonomic groups. Richness among wetland vegetation indicators rises abruptly around
557 4000 cal. BP, coinciding with the onset of terrestrialisation, which likely created a
558 diversity of habitat patches of peatland surface and open water. Diatom richness was
559 highest in the zone with predominantly benthic species (*Pinnularia-Orthoseira* zone)
560 and corresponds to more minerotrophic conditions and the absence of competing
561 *Pediastrum*. Among midges (chironomids) and mites, the greatest richness occurs in the
562 most recent zone (*Tanytarsus-Psectrocladius*), which is likely related to increased
563 temperatures and greater effective moisture. For testate amoebae, constant-sum and
564 accumulation-rate rarefaction results are in close agreement, indicating a steady rise in
565 richness through the last 8000 years that tracks the inferred expansion of oligotrophic
566 conditions (Figs 4 and S6).

Population-level instability is apparently linked to higher community diversity, as suggested by positive correlations between diversity estimates and population changes (Fig. 5). Correlations are strongest for testate amoebae ($r^2$: 0.38) and wetland vegetation ($r^2$: 0.29). These long-term observations appear to support theoretical predictions and previous empirical observations from shorter-term ecological studies (Tilman 1996; Loreau & de Mazancourt 2013; Gross et al. 2014). Highly diverse systems experience greater population-level variation after a disturbance due to interspecific competition. The effects of this competition on overall community structure and biomass are to lend stability, either because there is a greater probability that disturbance-resistant species will be present compared to a low-diversity system (Tilman 1996) or because species responses to disturbance occur at different times and rates (Loreau & de Mazancourt 2013).

Surprisingly, random walk simulations produce comparable relationships between richness and population change (Fig. 5). The relationship is stronger ($r^2$: 0.16) for a simulated population size of 500 compared to 2000 ($r^2$: 0.05), replicating correlations observed in the fossil communities. In communities with a low overall population, increases in richness are likely to be accompanied by significant changes in population sizes as new species migrate into the community. This effect is diluted in larger, more diverse communities in which many populations are already present and interspecific interactions may be more critical.

Our results, while representing conditional support for the richness and stability relationships observed in short-term studies, suggest that there is greater scope for testing ecological theories using long-term ecological data, model simulations and alternative indices of diversity and stability.

## Conclusions

Population dynamics theory makes important predictions that are notoriously difficult to test using short-term datasets. We analysed palaeoecological data from a peatland ecosystem to provide a long-term perspective on population dynamics. In accordance with predictions, populations of taxa that lived within the peatland tended to respond concurrently to internal changes, especially terrestrialisation. This pattern was not consistent through time, however, with both peatland and terrestrial taxa being impacted by external environmental changes such as major climatic shifts and human impacts at various times. The data show that antecedent population increases led to future population stability in two-thirds of cases. Random variation and inter-species competition emerged as likely explanations for population changes that did not conform to this theoretical prediction. This result highlights the need to integrate intracommunity interactions into population models and confront these with null models. As predicted, taxonomic groups of higher diversity tended to have greater community-level stability and population-level instability compared to low-diversity groups, although questions remain about how to best assess community stability. Future research should aim to expand knowledge of long-term population changes beyond a single site, aiming at replication on a regional scale.

## Author contributions

BA initiated and led the project; NM selected the study site; JL analysed pollen data; BA and WK described and dated the sediment; FC identified botanical macrofossils; AM analysed diatoms; BI and EI analysed chironomids; EM, YM, EADM, RJP and ML

analysed and interpreted testate amoebae; DC and EG collated data; and SC undertook numerical analyses and wrote the paper with assistance from all co-authors.

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**Data accessibility**

Complete datasets are given in Supporting Information and available through the Neotoma Paleoecology Database (Connor et al. 2017):

Geochronology https://apps.neotomadb.org/Explorer/?datasetid=22323

Plant macrofossil https://apps.neotomadb.org/Explorer/?datasetid=22324

Chironomid https://apps.neotomadb.org/Explorer/?datasetid=22325

Testate amoebae https://apps.neotomadb.org/Explorer/?datasetid=22326

Diatom https://apps.neotomadb.org/Explorer/?datasetid=22327

Loss-on-ignition https://apps.neotomadb.org/Explorer/?datasetid=22328

Charcoal https://apps.neotomadb.org/Explorer/?datasetid=22329

Pollen https://apps.neotomadb.org/Explorer/?datasetid=22330

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**FIGURES (see following pages)**

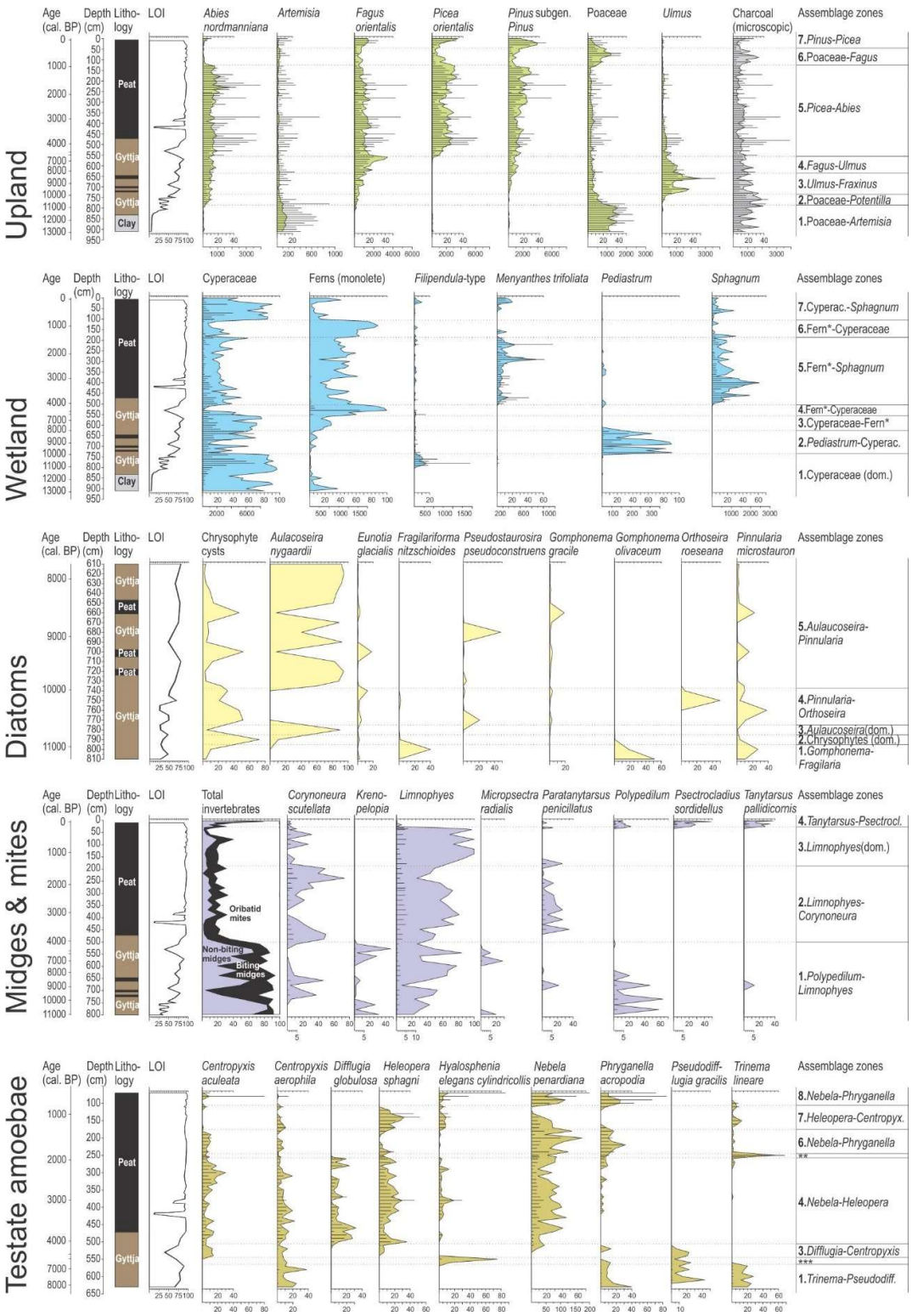


**Fig. 1.** Major taxa from the various taxonomic groups at Didachara, southern Georgia. Data are presented in stratigraphical order in both percentages (filled curves) and

accumulation rates (bars); x-axes are scaled independently for accumulation-rate data (lower scales: remains $cm^{-2}$ $yr^{-1}$). Ages, depths, lithology and loss-on-ignition (LOI) results are given on the left side; assemblage zones are given on the right. Further details in Table S1 and Figs S3 and S4.

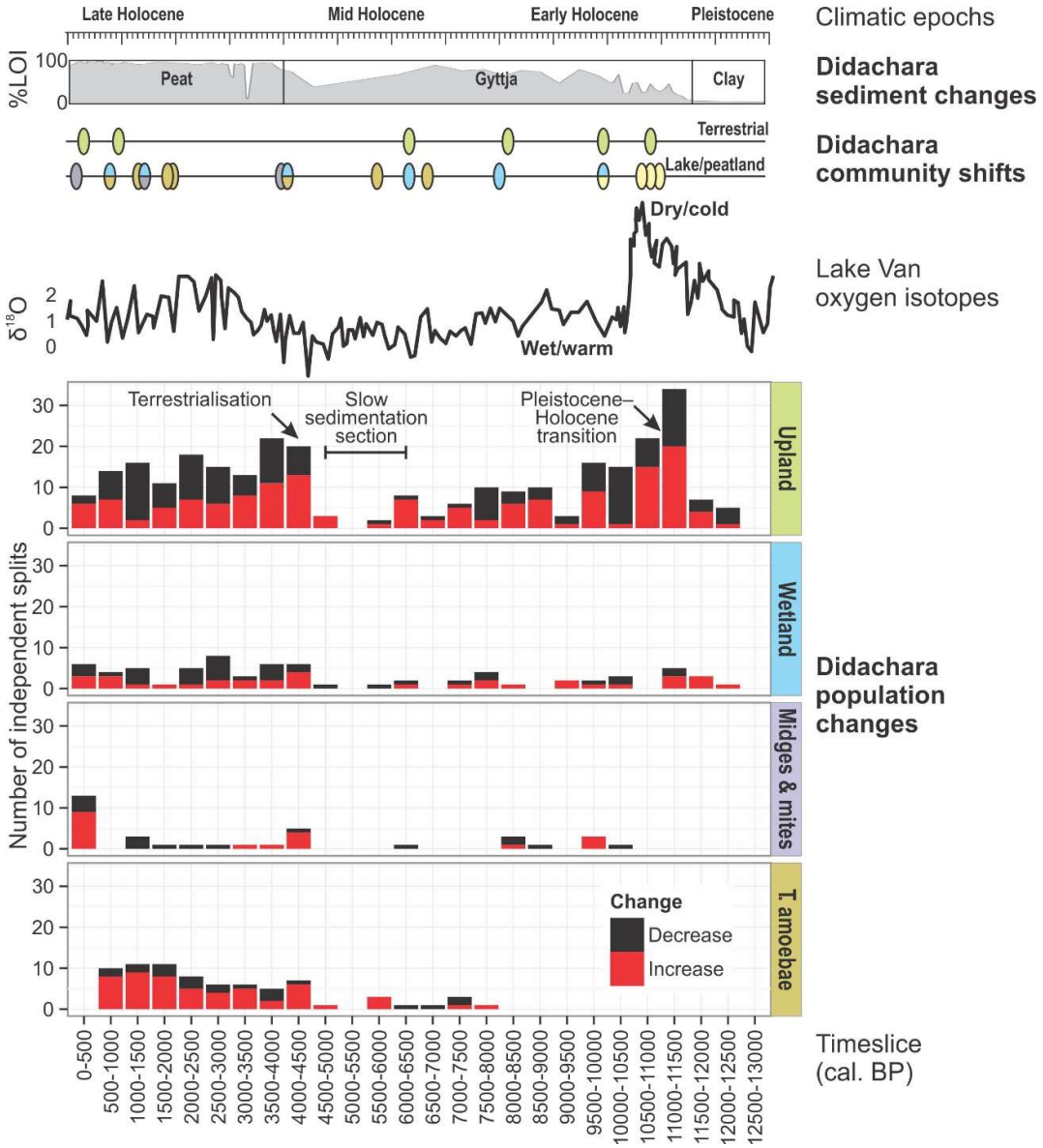


**Fig. 2.** The Lake Van palaeoclimatic record (Wick et al. 2003) compared to significant changes in taxonomic groups (ellipses) and the direction of palaeo-population changes

1039 at Didachara (histograms). Ellipses represent significant assemblage-zone boundaries
1040 (Fig. 1); histograms represent the number of independent splits in each 500-year
1041 timeslice with a detected increase or decrease in mean accumulation rates. Diatoms
1042 were not included as accumulation rates could not be determined. Organic content (loss-
1043 on-ignition) results are shown in grey.

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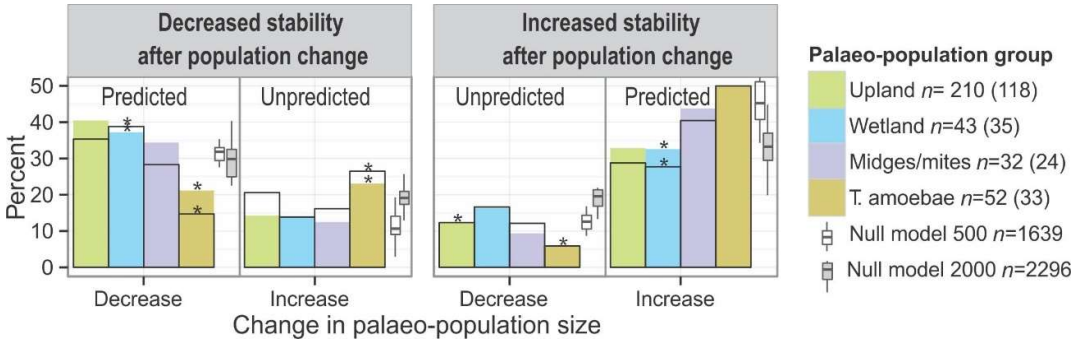


1045

1046 **Fig. 3.** Testing population dynamics theory with palaeo-population data. The graphs
1047 indicate the percentage of major population changes that show an increase or decrease
1048 in stability following a change in palaeo-population size. 'Predicted' responses accord
1049 with population dynamics theory, in contrast to 'unpredicted' responses. Hollow
1050 histograms show results for the more abundant taxa only (number of observations *n*
1051 given in parentheses). Box plots indicate random walk simulations with population sizes
1052 of 500 (representative of local proxies) and 2000 (representative of upland pollen:
1053 Blaauw et al. 2010). Asterisks denote observations that exceed 95% confidence
1054 intervals.

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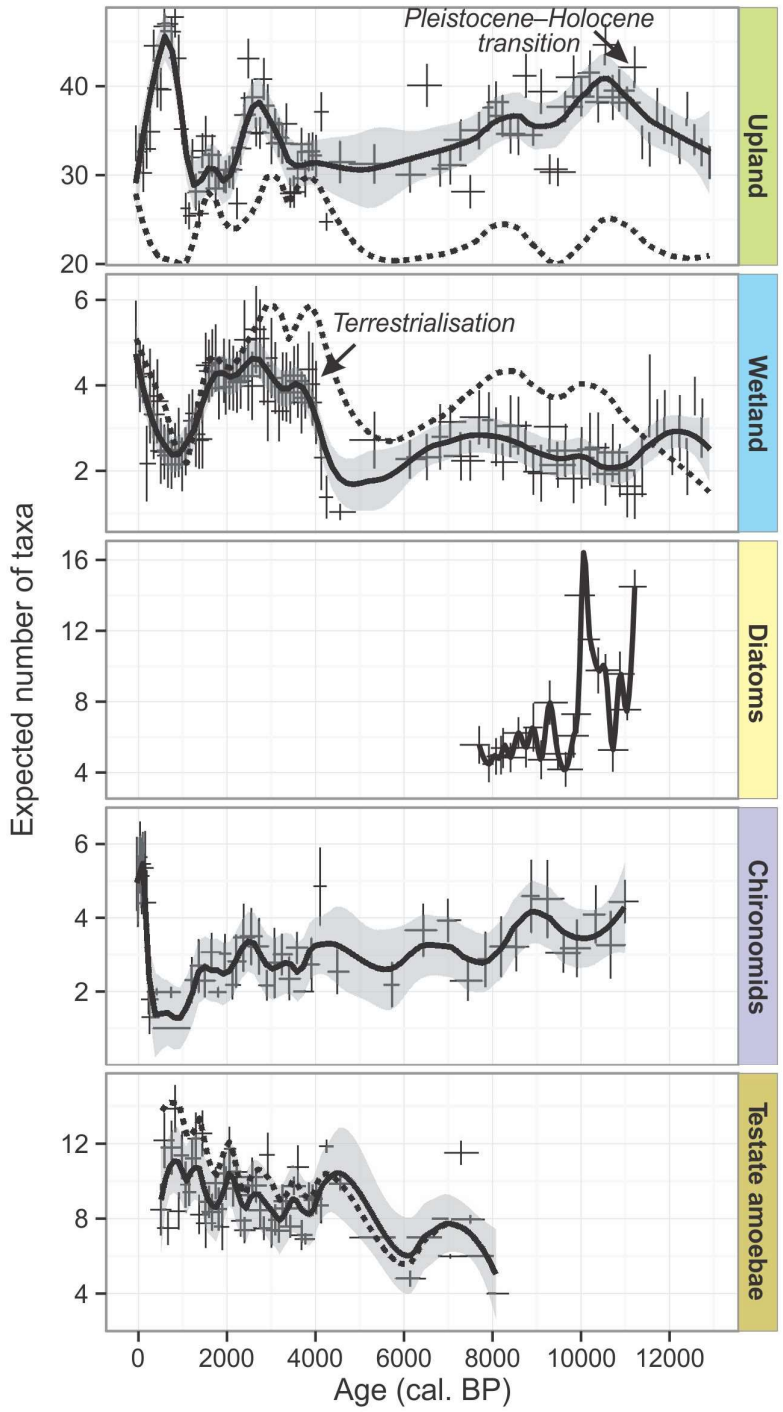


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1057 **Fig. 4.** Diversity trends in each of taxonomic groups at Didachara. Rarefaction results

1058 show estimated changes in richness for each fossil assemblage plotted by age; solid

1059 lines are smoothed constant-sum rarefaction estimates (Lowess span=0.2, with 95%

confidence intervals shaded); dotted lines are smoothed accumulation-rate rarefaction estimates (after van der Knaap, 2009).

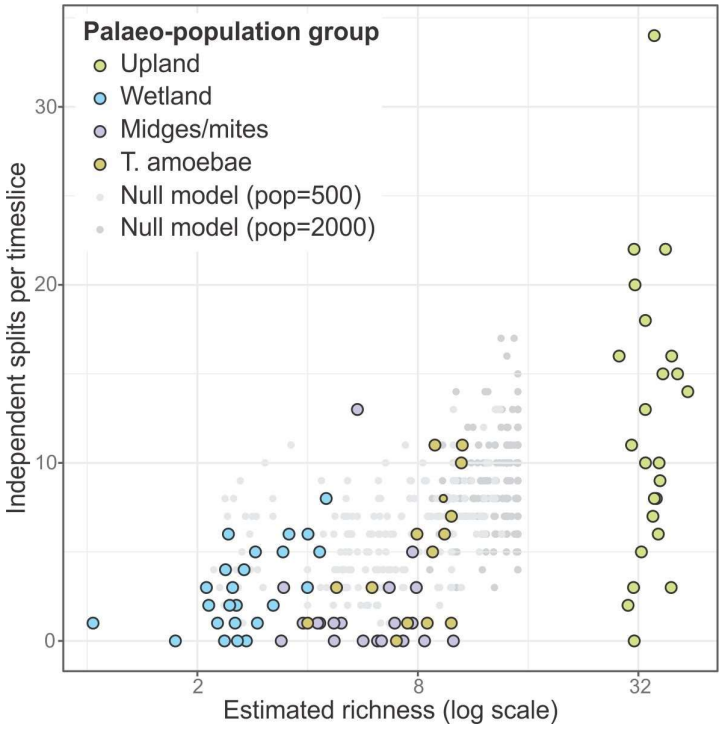
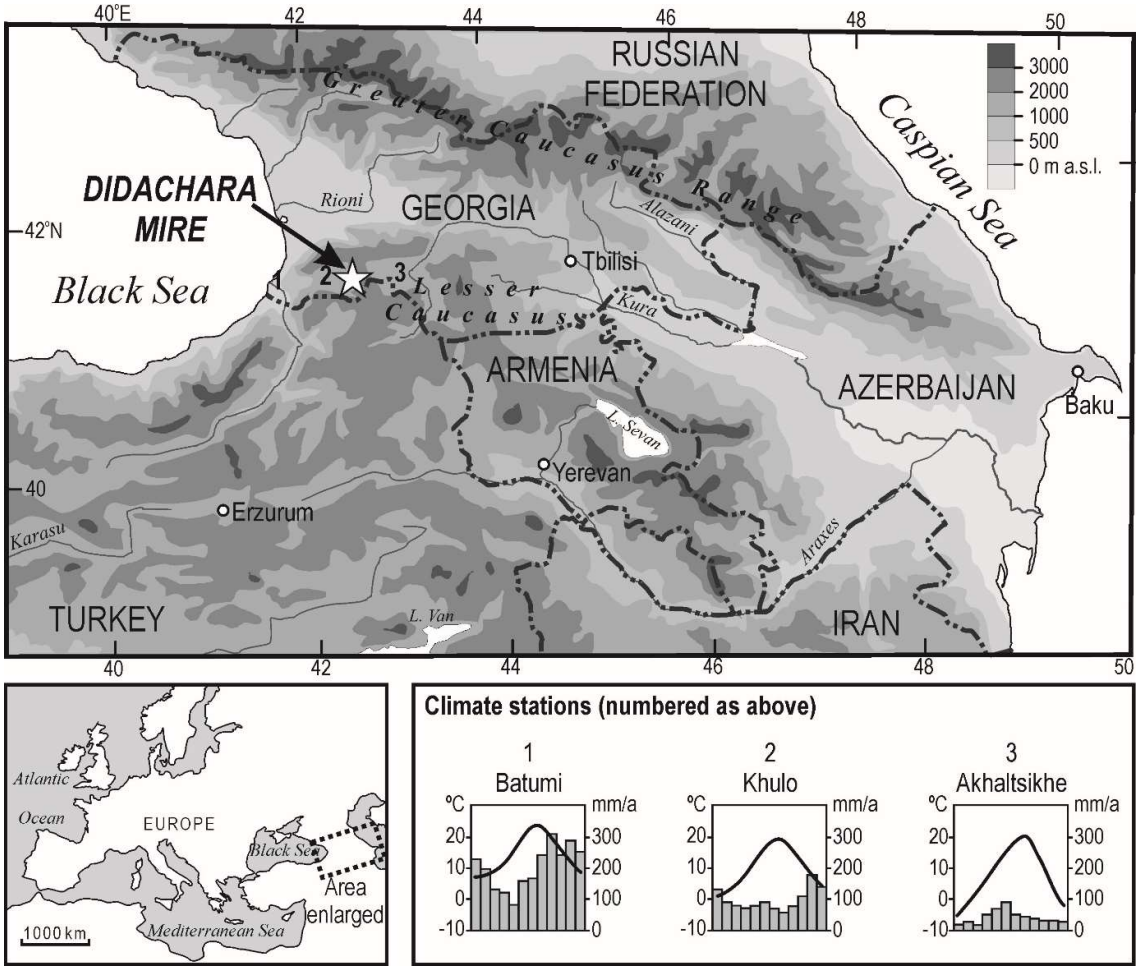



**Fig. 5**. Relationship between community-level richness (Fig. 4) and population-level instability (number of independent splits: Fig. 2). Timeslices as in Fig. 2. Random walk simulations (maximum richness 15) shown for comparison.

## SUPPORTING INFORMATION




1070

1071 Figure S1 *Location and climatic information for the study site*.

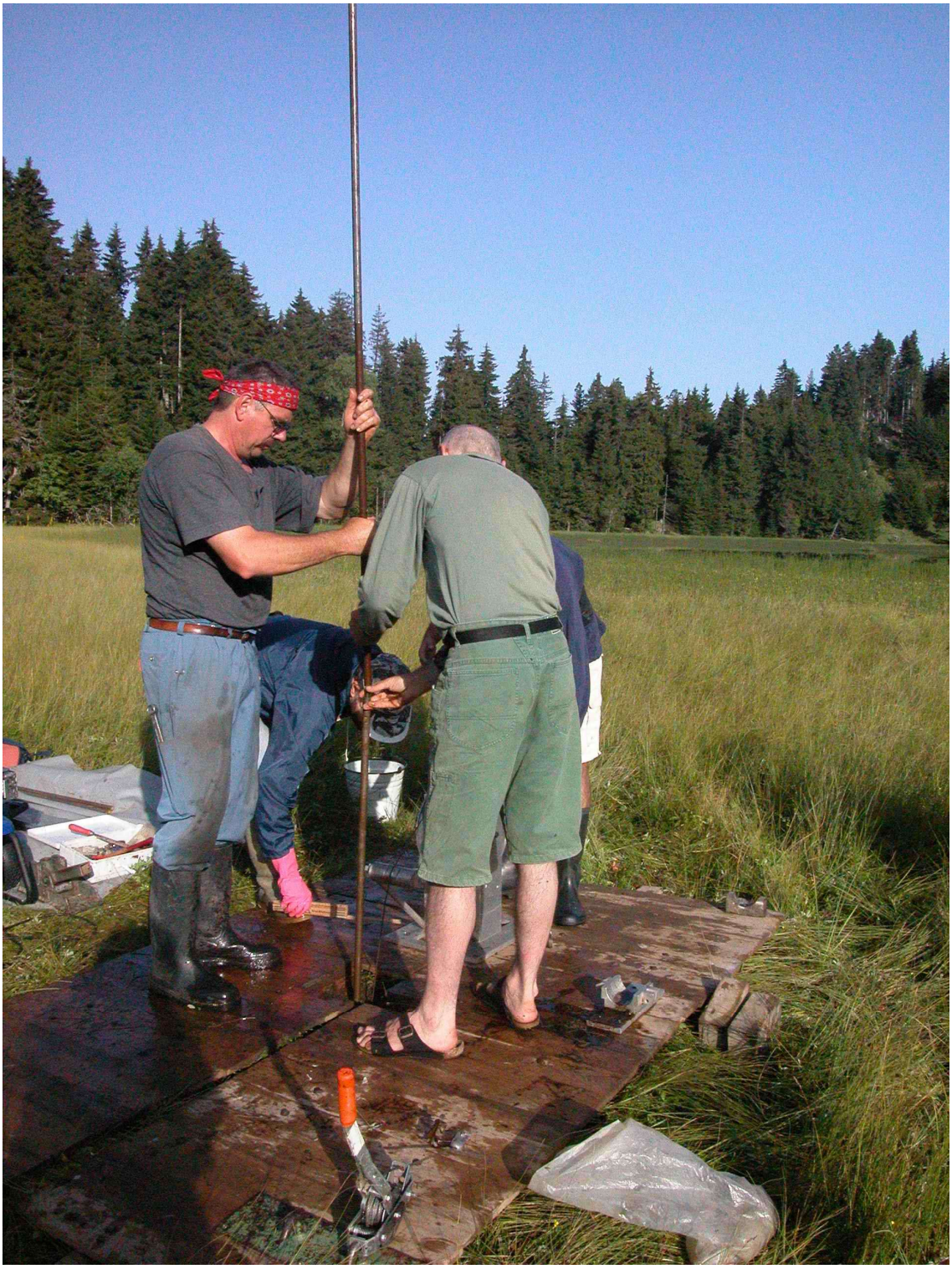


Figure S2 *Photograph of coring the study site, Didachara Mire in the Lesser Caucasus.*

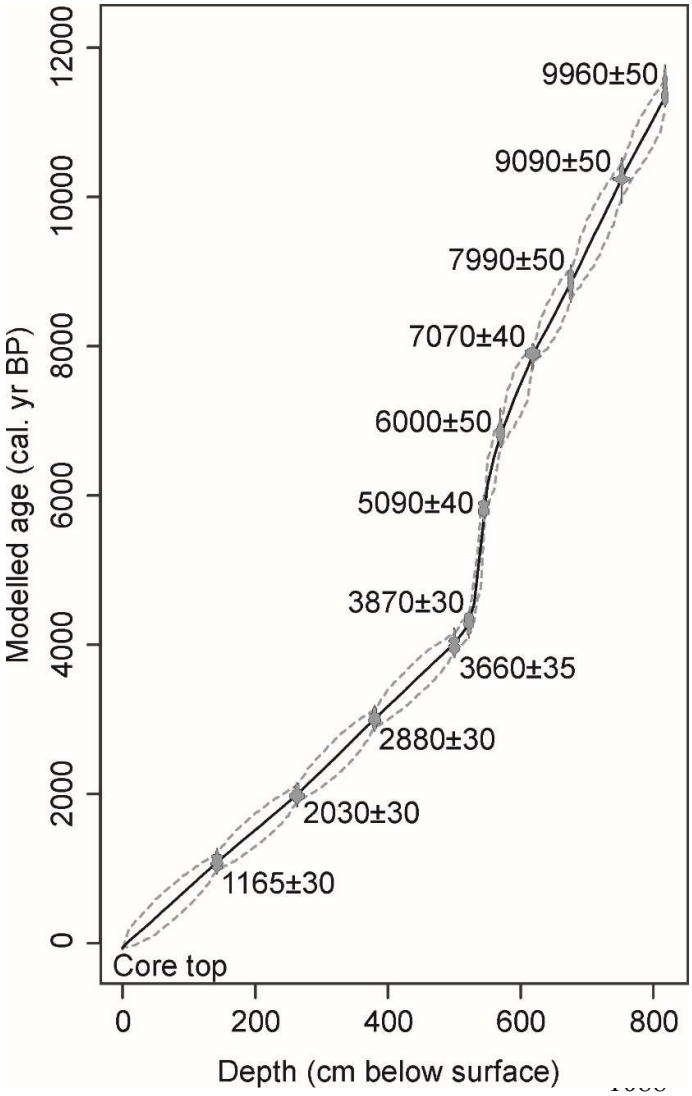



Figure S3 *Modelled age–depth relationship for Didachara Core C, with weighted mean age (solid line) and 95% confidence intervals (dotted lines). Uncalibrated ages and errors (Table S2) are given alongside modelled age distributions for each dated level (in calibrated years before present).*

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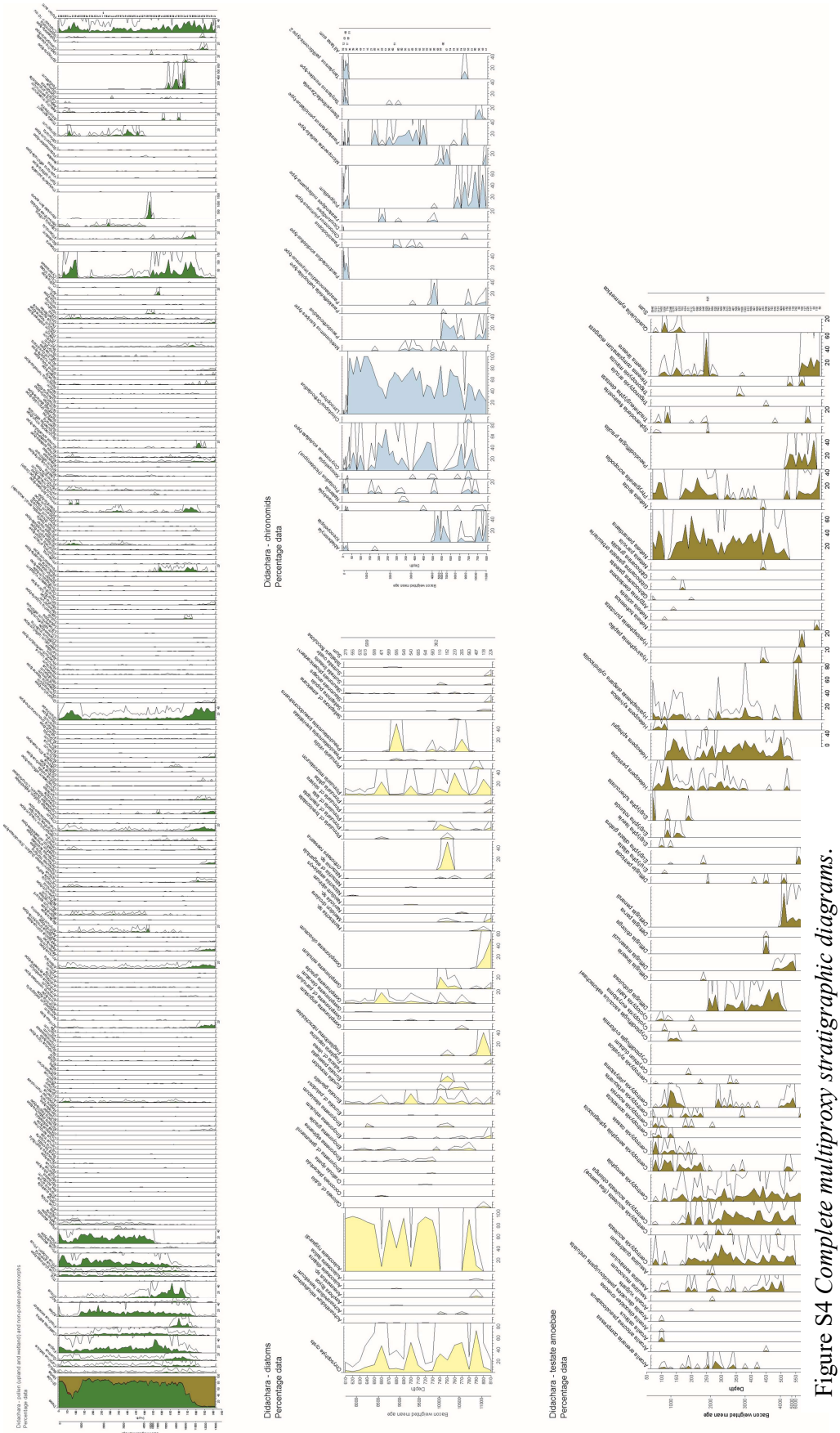
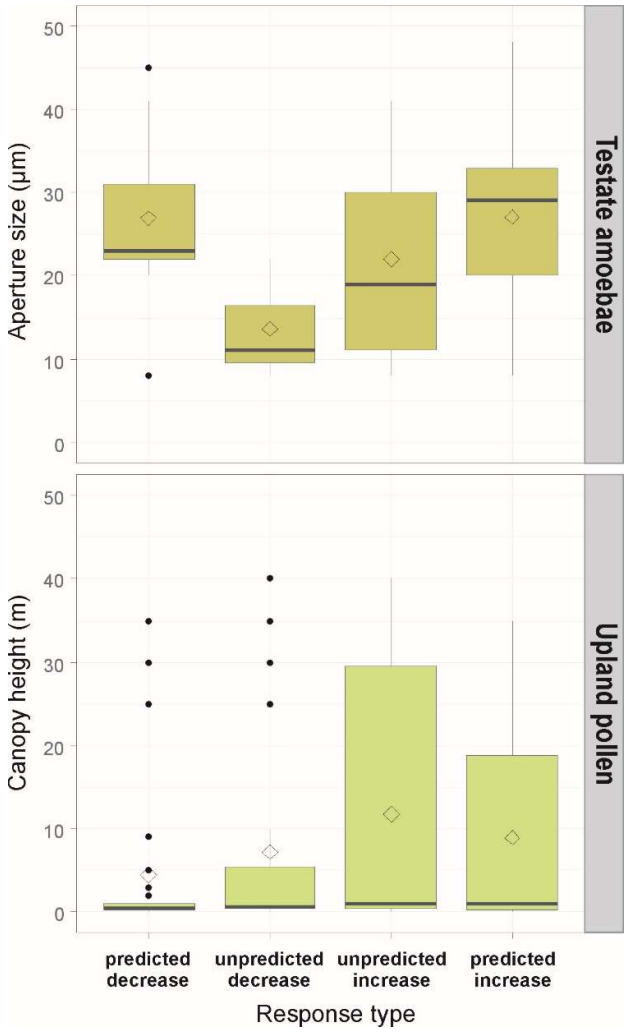



Figure S4 *Complete multiproxy stratigraphic diagrams.*

1093




1094

1095 Figure S5 *Organism size in relation to population response. 'Predicted' responses are*

1096 *those that align with theoretical predictions from population dynamics theory,*

1097 *contrasting with 'unpredicted' responses. Testate amoebae traits derived from Fournier*

1098 *et al. (2015); plant traits from Kleyer et al. (2008) – see Table S3.*

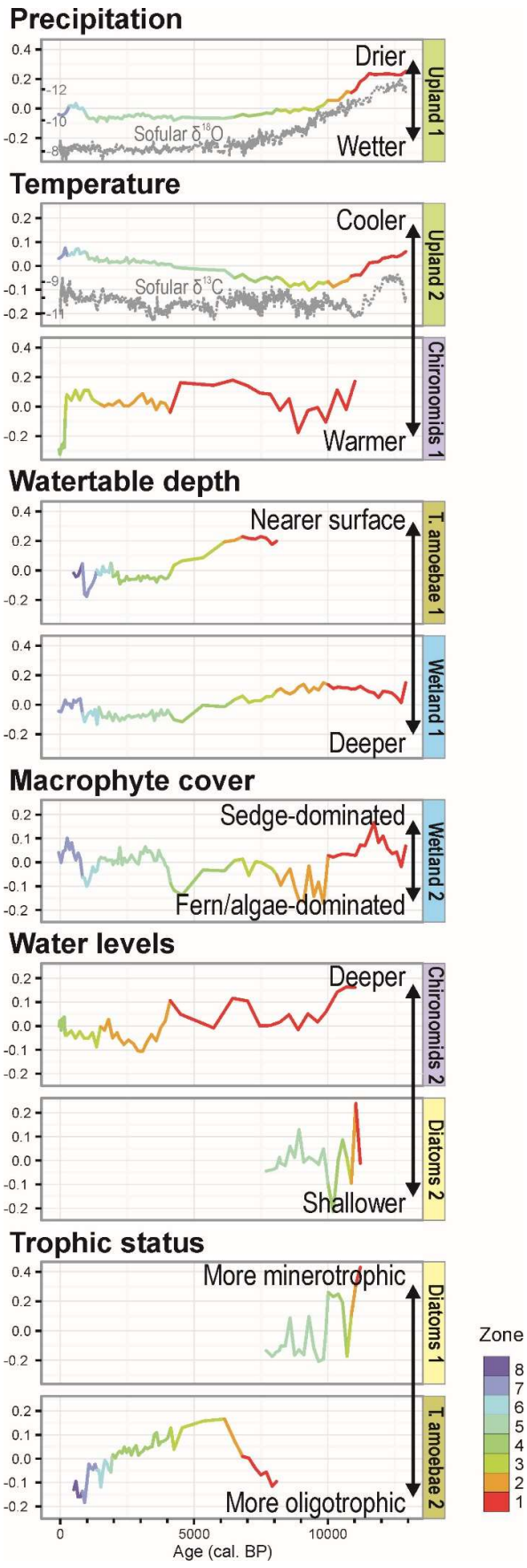
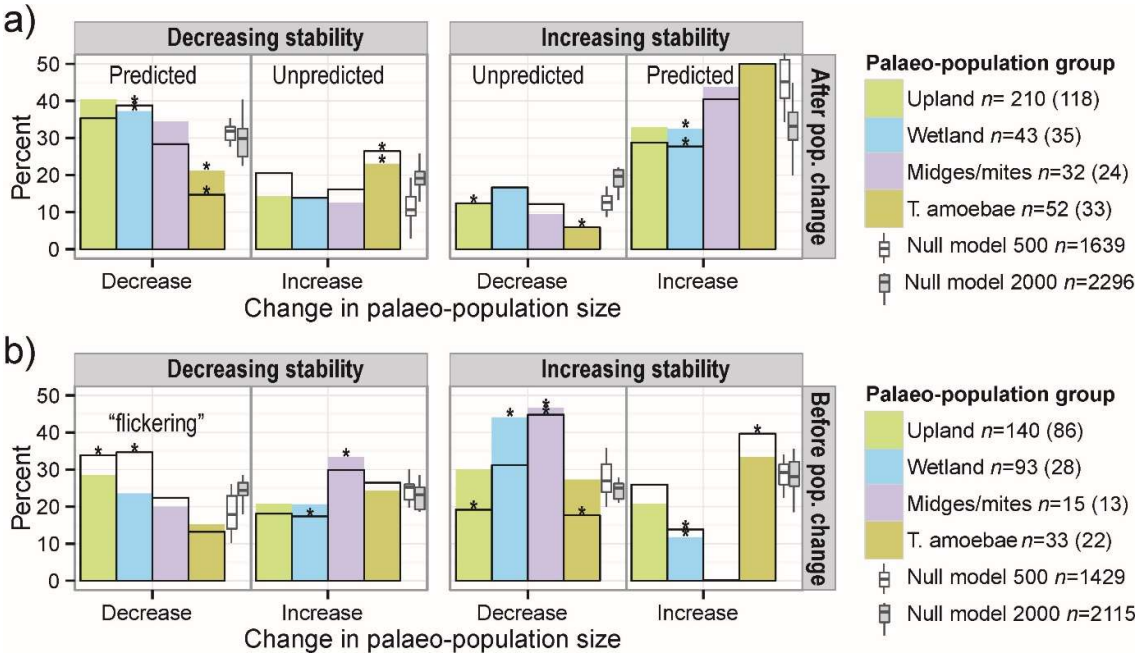



Figure S6 *Major community-level trends in each taxonomic group. Non-metric multidimensional scaling (NMDS) ordination results are grouped by relevant environmental variables; assemblage zones (Fig. 1) indicated by colours. Independent palaeoclimatic trends from the Sofular speleothem (Göktürk et al. 2011) are shown in grey in the upper panels for comparison.*




1114

1115 Figure S7 *Testing population dynamics theory with palaeo-population data. Histograms*

1116 *indicate the percentage of major population changes that a) show an increase or*

1117 *decrease in stability following a change in palaeo-population size; and b) show a*

1118 *change in population size following a change in stability. 'Predicted' responses accord*

1119 *with population dynamics theory, in contrast to 'unpredicted' responses. Hollow*

1120 *histograms show results for the more abundant taxa only (number of observations n*

1121 *given in parentheses). Results of random walk simulations are shown as box plots.*

1122

1123

Table S1 *Detailed lithological description*.

N.B. “sharp” and “gradual” refer to the lower boundary

| Depth (cm) | Colour (Munsell) | Lithological description |
|---|---|---|
| 0–337 | 10YR3/2 | Fen peat; wood remains at 248–254 and 260–263 cm |
| 337–409 | 10YR3/2 | Very decomposed fen peat (gradual lower boundary) |
| 409–423 | 10YR3/2 | Transition (gradual) |
| 423–472 | 10YR3/2 | Fen peat; wood remains at 440–445 cm (sharp) |
| 472–521 | 10YR3/2 | Dark, fine detritus gyttja; wood at 519–521 cm (sharp) |
| 521–524 | 10YR3/2 | Compact, coarse detritus gyttja (gradual) |
| 524–528 | 10YR3/2 | Dark, fine detritus gyttja (gradual) |
| 528–536 | 10YR3/2 | Silty, fine detritus gyttja |
| 536–639 | 10YR3/2 | Dark, fine detritus gyttja; rootlets at 559–570 cm (gradual) |
| 639–647 | 10YR3/2 | Dark-brown gyttja |
| 647–661 | 10YR3/2 | Fen peat |
| 661–698 | 10YR3/2 | Dark-brown gyttja; wood at 672 cm |
| 698–705 | 10YR3/2 | Fen peat |
| 705–718 | 10YR3/2 | Dark, coarse detritus gyttja |
| 718–724 | 10YR3/2 | Fen peat |
| 724–754 | 10YR3/2 | Dark-brown gyttja |
| 754–763 | 10YR4/3 | Beige-brown gyttja |
| 763–778 | 10YR4/2 | Grey-brown gyttja |
| 778–811 | 10YR3/1 | Dark-brown gyttja |
| 811–829 | 10YR3/1 | Gyttja with a few pebbles |
| 829–832 | 10YR3/1 | Transition: gyttja, some pebbles |
| 832–838 | 10YR3/2 | Grey-brown clay gyttja, some silt and sand |
| 838–840 | 10YR3/3 | Transition |
| 840–860 | 10YR4/3 | Dark, beige-brown clay gyttja, some coarse sand |
| 860–875 | 10YR5/3 | Grey-brown silt and clay, some coarse sand and pebbles |
| 875–914 | 10YR5/6 | Orange-grey silt and clay, some coarse sand and pebbles |

Table S2 *Radiocarbon dates*.

| Depth (cm) | Material dated | Laboratory number | $^{14}$C age (uncal. BP) | Calibrated age range (2-sigma, >5% probability) |
|---|---|---|---|---|
| 142–143 | *Sphagnum* | Poz-17137 | 1165±30 | 985–1032, 1047–1177 |
| 263 | *Picea* wood | Poz-15076 | 2030±30 | 1917–2061 |
| 380 | *Picea* wood | Poz-15093 | 2880±30 | 2922–3078 |
| 500 | Woody twig | Poz-15094 | 3660±35 | 3892–4087 |
| 522 | *Picea* wood | Poz-15095 | 3870±30 | 4229–4413 |
| 544–545 | Wood | Poz-21032 | 5090±40 | 5745–5916 |
| 569–570 | Wood, *Carex* | Poz-21029 | 6000±50 | 6725–6973 |
| 618 | Woody twig | Poz-17138 | 7070±40 | 7827–7971 |
| 675–676 | *Acer* twig | Poz-15096 | 7990±50 | 8698–9007 |
| 752–753 | Woody twig | Poz-17139 | 9090±50 | 10184–10303, 10313–10389 |

| | | | | | |
|---|---|---|---|---|---|
| 817–818 | Wood | Poz-15098 | 9960±50 | 11246–11615 | |

Table S3 *Traits associated with fossil taxa.*

Testate amoebae – fossil taxa and equivalents for trait analysis

| Fossil taxon | Taxon from which traits were derived (Fournier et al. 2015) |
|---|---|
| *Assulina seminulum* | *A. seminulum* |
| *Centropyxis aculeata* | *C. aculeata* |
| *Centropyxis aculeata* spineless | [not included] |
| *Centropyxis aculeata oblonga* | *C. aculeata oblonga* |
| *Centropyxis aerophila* | *C. aerophila* |
| *Centropyxis aerophila sphanicola* | *C. aerophila sphanicola* |
| *Centropyxis cassis* | *C. cassis* |
| *Centropyxis constricta* | *C. constricta* |
| *Centropyxis ecornis* | *C. ecornis* |
| *Centropyxis orbicularis* | *C. orbicularis* |
| *Centropyxis platystoma* | *C. platystoma* |
| *Centropyxis sylvatica* | [not included] |
| *Difflugia masaruzii* | [not included] |
| *Difflugia penardi* | *D. penardi* |
| *Euglypha tuberculata* | *E. tuberculata* |
| *Heleopera petricola* | *H. petricola* |
| *Heleopera sphagni* | *H. sphagni* |
| *Heleopera sylvatica* | *H. sylvatica* |
| *Hyalophenia elegans cylindricollis* | *H. elegans* |
| *Longinebela [Nebela] pernardiana* | *N. pernardiana* |
| *Phyrganella acropodia* | *P. acropodia* |
| *Tracheleuglypha dentata* | *T. dentata* |
| *Trinema lineare* | *T. lineare* |

Upland pollen – fossil taxa and equivalents for trait analysis (where several trait values were reported for an individual species, the median value was adopted)

| Fossil taxon | Taxon from which traits were derived (Kleyer et al. 2008) |
|---|---|
| *Betula* | *B. pendula* |
| *Quercus* | *Q. cerris* |
| *Fagus* | *F. sylvatica* |
| *Castanea* | *C. sativa* |
| *Fraxinus* | *F. excelsior* |

| | | |
|---|---|---|
| 1209 | *Abies* | *A. nordmanniana* |
| 1210 | *Acer* | *A. pseudoplatanus* |
| 1211 | *Ulmus* | *U. glabra* |
| 1212 | *Tilia* | *T. cordata* |
| 1213 | *Alnus glutinosa* | *A. glutinosa* |
| 1214 | *Corylus avellana* | *C. avellana* |
| 1215 | *Pinus* | *P. sylvestris* |
| 1216 | *Sorbus* | *S. aucuparia* |
| 1217 | *Picea* | *P. omorika* |
| 1218 | *Picea* stomata | [not included] |
| 1219 | *Ostrya* | [data from Flora of Georgia] |
| 1220 | *Juglans* | *J. regia* |
| 1221 | *Prunus* | *P. spinosa* |
| 1222 | *Ephedra distachia* | [data from Flora of Georgia] |
| 1223 | *Juniperus* | *J. communis* |
| 1224 | *Rhamnus* | *R. catharticus* |
| 1225 | *Salix* | *S. caprea* |
| 1226 | *Vitis* | [data from Flora of Georgia] |
| 1227 | *Achillea* | *A. ptarmica* |
| 1228 | *Aconitum* | [data from Flora of Georgia] |
| 1229 | *Anthericum* | *A. liliago* |
| 1230 | *Anthriscus sylvestris* | *A. sylvestris* |
| 1231 | *Artemisia* | *A. vulgaris* |
| 1232 | *Aster* | *A. tripolium* |
| 1233 | *Astrantia* | *A. major* |
| 1234 | *Athyrium filix-femina* | *A. filix-femina* |
| 1235 | *Blechnum spicant* | *B. spicant* |
| 1236 | *Bupleurum* | [data from Flora of Georgia] |
| 1237 | *Campanula* | *C. glomerata* |
| 1238 | *Carduus* | *C. crispus* |
| 1239 | *Centaurea scabiosa* | *C. scabiosa* |
| 1240 | *Cerealia* | *Secale* |
| 1241 | *Chaerophyllum* | *C. hirsutum* |
| 1242 | Chenopodiaceae | *Atriplex* |
| 1243 | *Cirsium* | *C. arvense* |
| 1244 | Cichorioideae | *Taraxacum* |
| 1245 | Cruciferae/Brassicaceae | *Capsella bursa-pastoris* |
| 1246 | *Dipsacus* | *D. lacinatus* |
| 1247 | *Dryopteris* | *D. filix-mas* |
| 1248 | *Echium* | *E. vulgare* |
| 1249 | *Epilobium* | *E. hirsutum* |
| 1250 | *Falcaria* | *F. vulgaris* |
| 1251 | *Geranium* | *G. robertianum* |
| 1252 | *Geum* | *G. urbanum* |
| 1253 | Gramineae-Poaceae | *Phleum phleoides* |
| 1254 | *Gnaphalium* | *G. luteo-album* |
| 1255 | *Heracleum* | *H. sphondylium* |
| 1256 | *Humulus* | [data from Flora of Georgia] |
| 1257 | *Hypericum* | *H. perforatum* |
| 1258 | *Mentha* | *M. arvensis* |

| | | |
|---|---|---|
| 1259 | *Minuartia* | *M. hybrida* |
| 1260 | *Pedicularis* | *P. palustris* |
| 1261 | *Peucedanum* | *P. palustre* |
| 1262 | *Phyteuma* | *P. spicatum* |
| 1263 | *Pimpinella* | *P. saxifraga* |
| 1264 | *Plantago alpina* | *P. coronopus* |
| 1265 | *Plantago lanceolata* | *P. lanceolata* |
| 1266 | *Pollen (indet.)* | [not included] |
| 1267 | *Polygonum aviculare* | *P. aviculare* |
| 1268 | *Potentilla* | *P. reptans* |
| 1269 | *Pteridium* | *P. aquilinum* |
| 1270 | *Ranunculus acris* | *R. acris* |
| 1271 | *Rubiaceae* | *Galium verum* |
| 1272 | *Rumex obtusifolius* | *R. obtusifolius* |
| 1273 | *Sanguisorba minor* | *S. minor* |
| 1274 | *Sedum* | *S. acre* |
| 1275 | *Senecio* | *S. vulgaris* |
| 1276 | *Silene dioica* | *S. dioica* |
| 1277 | *Silene vulgaris* | *S. vulgaris* |
| 1278 | *Symphytum* | *S. officinale* |
| 1279 | *Thalictrum* | *T. minus* |
| 1280 | Umbelliferae/Apiaceae | *Torilis arvensis* |
| 1281 | *Urtica* | *U. dioica* |
| 1282 | *Veratrum* | *V. album* |
| 1283 | | |
| 1284 | | |